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IDENTIFICATION OF QTL FOR PRODUCTION TRAITS IN CHICKENS

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IDENTIFICATION OF QTL FOR PRODUCTION TRAITS IN CHICKENS

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If the poultry industry hopes to continue to flourish, the identification of potential quantitative trait loci (QTL) for production-related traits must be pursued. This remains true despite the sequencing of the chicken genome. In view of this need, a scan of the chicken genome using 72 microsatellite markers was carried out on a meat-type × egg-type resource population measured for production and egg quality traits. Using a Bayesian analysis, potential QTL for a number of traits were identified on several chromosomes. Evidence of eight QTL regions associated with a total of eight traits (specific gravity, albumin height, Haugh score, shell shape, total number of eggs, final body weight, gain, and feed efficiency) was found. Two of these regions, one spanning the area of 263/287 cM on GAA01 and the other spanning the area of 23/28 cM on GAA02, were associated with multiple QTL.

Keywords: Microsatellite; Quantitative trait loci; Production trait; Chicken

INTRODUCTION

Poultry meat and eggs continue to be very important agricultural commodities not only in the United States, but worldwide. Primarily due to advanced breeding programs, tremendous progress in production traits has been made to meet the growing demands of consumers. However, in order for the poultry industry to

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continue to flourish, advances in poultry genetics are essential and the identification of quantitative trait loci (QTL), especially for production traits, has to be pursued.

The chicken karyotype includes eight pairs of macrochromosomes, 30 pairs of microchromosomes, plus the sex chromosomes Z and W (1, 21). Linkage maps in poultry are now at the stage where they have sufficient density to make whole genome scans for QTL feasible. The chicken consensus map contains 1889 loci spanning 3800 cM, among which are many microsatellite markers ideally suited for use in such scans (4). While several studies have identified potential QTL in poultry for disease (e.g., 15, 25) and various production traits (e.g., 5, 6, 10, 12–14, 16–18), the resource population that we have been able to tap into has allowed us to perform a fairly comprehensive search for production trait QTL in these birds. This is the first important step in the effort to fine-map QTL that will provide a useful reference for further candidate gene research leading to the identification of the causative genes. It is hoped that the results will eventually allow for the development of genetic tests to help in the selection and breeding of even more highly productive chickens.

Methods of QTL mapping abound. The methods developed to date can generally be classified into one of three categories: least-squares analysis, maximum likelihood (ML) analysis, and Bayesian analysis. As was outlined by Yi and Xu (23), the various methods differ in their computational requirement, the efficiency with which they extract information, their flexibility to handle different data structures, and their ability to map multiple QTL. Bayesian analysis, while being computationally demanding, is very flexible in the use of full pedigrees and can map multiple QTL with multiple effects, including epistatic effects (22). It takes into account the uncertainties, such as the number and location of QTL, effects of QTL, and the genotypes of markers and QTL that are associated with all unknowns in the QTL mapping problem (23).

In this paper the results of a genome scanning approach aimed at the identification of potential QTL in a wide cross between a meat-type × egg-type resource population are presented. The traits analyzed included initial weight, final weight, specific gravity, egg weight, albumin height, Haugh score, shell shape, total eggs laid, gain, and feed efficiency, all of which are relevant to either the broiler or the layer chicken industry.

MATERIALS AND METHODS

Animal Resource

The resource population for this study was generated using existing highly characterized chicken strains developed at Agriculture and Agri-Food Canada's former Centre for Food and Animal Research in Ottawa. For the wide cross, a Cornish meat-type strain 21 and an inbred egg-type strain WG that differed greatly in their performance were chosen as the parental strains. Strain 21 was a Cornish-type meat-type sire strain that was synthesized from commercial sire strains in 1978 and selected subsequently for high growth rate and low abdominal fat from control strain 20 (7). Strain WG was a White Leghorn inbred line that had been selected from strain 9 for egg production and related traits as well as for Marek's disease resistance (3). Three strain 21 sires and 19 strain WG dams were used to produce 73 F_1 individuals. Only related F_1 progeny were crossed to produce the F_2 population. For this study, 192 female F_2 birds were included in the analysis of this cross. All birds were handled in a manner conforming to the guidelines set by the Canadian Council on Animal Care.

DNA Samples

Blood samples were collected from all sires and dams, F_1 and F_2 birds, and frozen after collection. Blood samples were diluted [25 µl of blood diluted with 175 µl of phosphate buffered saline (PBS)] prior to DNA extraction. DNA was extracted using a standard QIAGEN DNA extraction kit (QIAGEN Inc., Valencia, CA). Working DNA concentrations were adjusted to 30 ng/µl.

Genotyping

Genotyping of all birds was performed using 72 evenly spaced microsatellite markers providing approximately 50% genome coverage at 30 cM marker spacing (Table 1). Primer information for these markers can be obtained from the U.S. Poultry Genome Project website at http://poultry.mph.msu.edu. All microsatellites were amplified by PCR using a standard thermocycling protocol consisting of an initial denaturing phase of 94°C for 3 min followed by 35 cycles of 94°C for 1 min, 45°C for 1 min, and 72°C for 1 min and ending with an elongation phase of 5 min at 72°C. Primers were labeled with FAM, TET, or HEX fluorescent dyes and all amplified fragments were run on a 4% denaturing polyacrylamide gel using an ABI PRISM 377 automatic sequencer (Applied Biosystems, Foster City, CA). Gels were tracked manually and extracted using the Genescan analysis software and then scored. All data were verified after initial scoring.

Phenotypic Data

Phenotypic data on all birds were collected at Agriculture and Agri-Food Canada in Ottawa between 1993 and 1995. Traits recorded and analyzed included specific gravity (SGRAV; recorded after subtracting from the actual specific gravity reading a 1.0 and multiplying the residual by 100), egg weight (EGG_WGT; recorded in grams), albumin height (ALB_HGT; measured in millimeters), Haugh score (HAUGH; calculated according to Wells [19], shell shape (SHELSHAP; the ratio of the width of the egg at its largest point to the egg's length at its longest point), total eggs produced (EGGTOT; sum of the eggs laid by a bird), initial body weight (INITBWT; body weight in decagrams at the beginning of the test period), final body weight (FINBWT; body weight in decagrams at the end of the test period, which was ~500 days of age), gain, and feed efficiency (FEEDEFF; Gain/feed consumed). Egg quality and production traits were analyzed from eggs collected over five days within each of three collection periods. For the analyses used in this study, data at ~240 days of age were used.

Statistical Analysis

Data were analyzed using the Bayesian method of QTL analysis for complicated mating design (20, 23). Although our resource population used an F_2 mating design, one parental line was not inbred. The analysis was complicated by the fact that three males from an outbred population were mated with 19 females from a near inbred line to generate the F_1 individuals. The mating of the F_1 individuals to form the F_2 mapping population was also complicated. Therefore, the pedigree analysis method of Xu and

Table 1 Molecular markers used in the genome scan of a meat-type by egg-type cross, their locations on the chromosomes, and the relative positions used for analysis

Chromosome or linkage group	Marker	Location (cM)[1]	Analysis position[2]	Chromosome	Marker	Location (cM)[1]	Analysis position[2]
1	ADL0160	34	0	4	ADL0143	0	0
1	MCW0010	84	50	4	ADL0317	12	12
1	ADL0019	127	93	4	ADL0145	70	70
1	ADL0124	141	107	4	ADL0246	121	121
1	ADL0192	153	119	4	ADL0266	137	137
1	ADL0150	196	162	4	ADL0331	177	177
1	ADL0361	217	183	5	ADL0253	27	0
1	ADL0314	246	212	5	ADL0187	135	108
1	LEI0217	270	236	5	ADL0166	153	126
1	UMA1.126	300	266	6	ADL0323	0	0
1	ADL0134	346	312	6	ADL0230	49	49
1	ADL0183	397	363	6	ADL0244	60	60
1	ADL0198	418	384	7	ADL0315	25	0
1	ADL0122	450	416	7	ADL0279	32	7
2	ADL0228	4	0	7	MCW0133	82	57
2	ABR0020	10	6	7	ADL0326	118	93
2	MCW0082	31	27	8	ADL0105	2	0
2	ADL0270	52	48	8	ADL0161	51	51
2	ADL0309	81	77	8	ADL0322	91	91
2	ADL0176	107	103	8	ADL0345	107	107
2	MCW0063	110	106	10	ADL0158	6	-
2	ADL0217	115	111	10	ADL0272	48	-
2	ADL0212	142	138	11	ADL0210	27	-
2	ADL0257	145	141	11	ADL0308	31	-
2	ADL0157	258	254	12	ADL0240	2	-
2	ADL0236	318	314	12	ADL0044	31	-
2	MCW56	405	401	13	ADL0310	62	-
2	LEI0070	450	446	14	MCW0062	44	-
2	ADL0146	460	456	17	ADL0149	58	-
3	MCW0169	44	0	18	ADL0304	12	-
3	ADL0155	141	97	23	ADL0262	42	-
3	ADL0327	185	141	Z	ADL0022	16	-
3	ADL0115	222	178	Z	ADL0273	90	-
3	ADL0306	242	198	Z	ADL0250	98	-
3	ADL0237	301	257	E34	ADL0298	23	-
3	LEI0166	332	288	E46	MCW0157	29	-

[1]Based on the East Lansing genetic map (see http://poultry.mph.msu.edu).
[2]Only markers on chromosomes 1–8 could be successfully analyzed.

Yi (20) was adopted. The original method of Xu and Yi (20) was designed to map QTL responsible for both the population difference (fixed effect) and within population variance (random effect). Because the genetic variance among the female parents is negligible and the purpose of the QTL analysis is to detect QTL for the population difference, the within population variance was suppressed in the analysis.

In the Bayesian analysis, the user needs to provide the prior information for all the unknown parameters. These prior distributions were identical to what was

suggested by Yi and Xu (23). For example, a normal prior distribution was chosen for the QTL effect, a uniform distribution was chosen for the population mean, and a vague prior was chosen for the residual variance.

Bayesian analysis implemented via the MCMC algorithm also requires users to provide initial values for all parameters. The same starting values and prior distributions were used for analyses of all traits. The MCMC algorithm started with no QTL. The starting values for the overall mean and the residual variance were 0.0 and 2.0, respectively. The truncated Poisson prior for the number of QTL had a mean of $\mu = 3$ and a maximum number of $l_{\max} = 8$. The prior for the overall mean is uniform in the range of $[-4, 4]$. The residual variance takes a uniform prior with a range of $[0, V_P]$, where $V_P = 2$ is approximately equal to twice the phenotypic variance calculated from the data. The priors for all QTL allelic and dominance effects were chosen to be normal $N(0, V_p/2)$. Finally, the tuning parameters of proposals in the Metropolis-Hastings sampling were chosen to be 2.0 cM for QTL locations and 0.05 for all other parameters.

The proposed MCMC sampler was run for 10^6 cycles in each of the MCMC analyses after discarding the first 2000 cycles for the burn-in period. On a Sun SPARC 5 workstation, the analyses with a MCMC chain of 400,000 took about 6 h for each trait. The chains were thinned (saved one iteration in every 20 cycles) to reduce serial correlation in the stored samples so that the total number of samples kept in the post-Bayesian analysis was 20,000 for each parameter. The stored samples were used to infer the statistical properties of the parameters.

QTL locations were inferred using the posterior QTL intensity function (11, 24). The whole chromosome was divided into many equidistant intervals, each with a length of 1 cM. The QTL intensity at each short interval is defined as the proportion of hits by a QTL among the posterior samples. For each of the QTL allelic and dominance effects, the average value within the short interval (1 cM) was calculated and plotted against the chromosomal position forming a location-wise posterior profile for each effect called the effect profile. For the candidate regions of QTL (regions repeatedly hit by QTL), the size of QTL effects can be visualized. Only chromosomes 1 (GGA01) to 8 (GGA08) were analyzed.

Data Standardization

Bayesian analysis implemented via the MCMC algorithm requires users to provide initial values for all unknown quantities (including parameters and missing values). The initial values, however, must be sufficiently robust so that the MCMC algorithm will converge within a reasonable time frame. A set of robust initial values can be found by analyzing traits that are standardized through linear transformations. We found that the standardization is important for analyzing traits with different scales of measurement. The standardization allows the same set of initial values to be used for analyzing all different traits. Trait standardization was obtained by

$$y^* = (y - \bar{y})/s_y,$$

where y is the trait value measured in the original scale, $\bar{y}$ is the sample mean of y calculated from all individuals included in the mapping population, and s_y is the sample

standard deviation. Our Bayesian analysis was actually performed on y^* rather than on y. Therefore, all parameter estimates were reported in the standardized scale. One may convert the parameter estimates back to the original scale simply by multiplying by the estimated effect by s_y.

RESULTS AND DISCUSSION

Many factors affect the successful application of marker-assisted selection in commercial poultry populations. The ability to identify genes or closely linked markers to the genes underlying QTL of interest is foremost among these. Some other important factors include whether or not it is possible to detect that allelic variation at these important loci is segregating in a population, as well as our ability to understand how these genes interact with the environment and other genes affecting traits of economic importance (8). In addition, the whole process must be done in a cost- and time-effective manner so as to make it feasible for use in an industry setting.

The microsatellite markers used in the present study are presented in Table 1 along with their chromosomal location and the relative positions used for the analyses. On average, 3.4 alleles were detected for each microsatellite locus used in the analysis with a range of 2 to 6 alleles per locus.

The means and standard deviations of the major traits analyzed are given in Table 2. Parameters associated with QTL identified on GGA01 to GGA08 are shown in Table 3, while chromosomal intensity profiles for the QTL identified are shown in Figure 1. As can be seen from the table and figure, evidence of eight QTL regions associated with a total of eight traits was found. The proportion of the variance explained by the QTL identified was low to moderate (0.07–0.25).

One of the main benefits of conducting a QTL analysis is to verify initial reports for trait associations, which would give higher confidence that a particular region contains one or more genes of interest. Previous studies have reported 75+ QTL for growth and body composition traits including 50+ QTL mapped on GGA01 to GGA08 (6, 10, 12, 14, 17). In our study, we examined two body weight–related traits, FINBWT and GAIN. QTL regions for both FINBWT

Table 2 The sample means and standard deviations of the traits analyzed for a meat-type by egg-type chicken cross

Trait	Sample size[1]	Mean	Standard deviation
SGRAV	229	838	60
EGG_WGT	229	580	45
ALB_HGT	229	704	96
HAUGH	229	840	57
SHELSHAP	229	39	5.4
EGGTOT	256	123	53
INITBWT	182	421	135
FINBWT	182	781	170
GAIN	182	360	51
FEEDEFF	182	3550	275

[1]Sample size is the number of individuals measured for the trait of interest (excluding individuals with missing values).

Table 3 Parameters of QTL identified for traits analyzed in a meat-type by egg-type cross using Bayesian analysis

Trait	Chr	Analysis position	Location (cM)[1]	Flanking markers	Additive effect	Dominance effect	H^2
SGRAV	2	14	23	ADL0228, MCW0082	5.6	40.4	0.19
ALB-HGT	1	239	270	ADL0314, UMA1.126	–25.1	54.7	0.17
	2	266	270	ADL0157, ADL0236	–51.6	–5.3	0.19
HAUGH	1	251	287	ADL0314, UMA1.126	−8.2	46.1	0.25
SHELLSHAP	8	42	42	ADL0105, ADL0161	0.5	–2.5	0.07
EGGTOT	1	116	149	ADL0019, ADL0150	–11.1	30.8	0.17
	2	115	117	ADL0176, ADL0257	–25.9	14.8	0.21
FINBWT	2	24	28	ADL0228, MCW0082	56.4	−52.9	0.10
	2	424	428	MCW0056, ADL0146	97.1	−88.2	0.23
GAIN	2	22	25	ADL0228, MCW0082	24.0	–10.1	0.12
FEEDEFF	1	230	263	ADL0314, UMA1.126	−64.6	109.4	0.11

[1]Based on the East Lansing genetic map (see http://poultry.mph.msu.edu).

(27 and 420 cM, respectively) and GAIN (25 cM) were found on GGA02. Tatsuda, Fujinaka, and Yamasaki (12) reported QTL for body weight at 13 and at 16 weeks of age at approximately 62 and 61 cM, respectively, of GGA02 which is fairly close to the QTL regions for FINBWT and GAIN (27 and 25 cM, respectively) identified in the present study. This region is also very similar to that of 40 cM reported by van Kaam et al. (17) for feed intake over a fixed weight interval, and 29 cM reported by Carlborg et al. (2) for body weight at 112 days of age. The QTL for FINBWT located to the area of 420 cM of GGA02 in the present study maps to the same region for body weight QTL at 200 days reported by Kerje et al. (6), and the QTL for body weight at 46 and 200 days reported by Carlborg et al. (2). Evidence of a QTL for FEEDEFF was mapped in the present study to the region of 263 cM of GGA01. This location compares favorably with a QTL for feed intake over a fixed weight interval that was mapped to 235 cM by van Kaam et al. (17).

With respect to egg production and quality traits, QTL were mapped in this study to GGA01, GGA02, and GGA08. The EGGTOT QTL on GGA01 (149 cM) is at a similar position as a QTL for egg production reported by Sasaki et al. (9). In addition to influencing FEEDEFF, the QTL on GGA01 (263 cM) accounts for ALB-HGT and HAUGH. Furthermore, an ALB-HGT QTL was mapped to GGA02 (270 cM). We were not able to confirm the QTL on GGA02 (70 to 120 cM) for Haugh units at 40 and 60 weeks of age reported by Tuiskula-Haavisto et al. (14). While there have been no reports of QTL for albumen quality at either of these two latter locations, Sasaki (9) has identified several QTL for egg shell strength, thickness, and weight that localize to GGA01 at position 330 cM. Interestingly, Tuiskula-Haavisto et al. (14) have reported a QTL influencing albumen quality at 40 weeks of age that maps to the same location as our EGGTOT QTL on GGA01.

QTL for SGRAV, EGGTOT, and SHELLSHAP map to GGA02 (23 cM), GGA02 (117 cM), and GGA08 (42 cM), respectively. All these QTL are new and, thus, represent areas for potential confirmation. However, the QTL on GGA08 has been previously found to be associated with number of eggs from 18 to 40 weeks of age (14) and many growth and body weight traits (2).

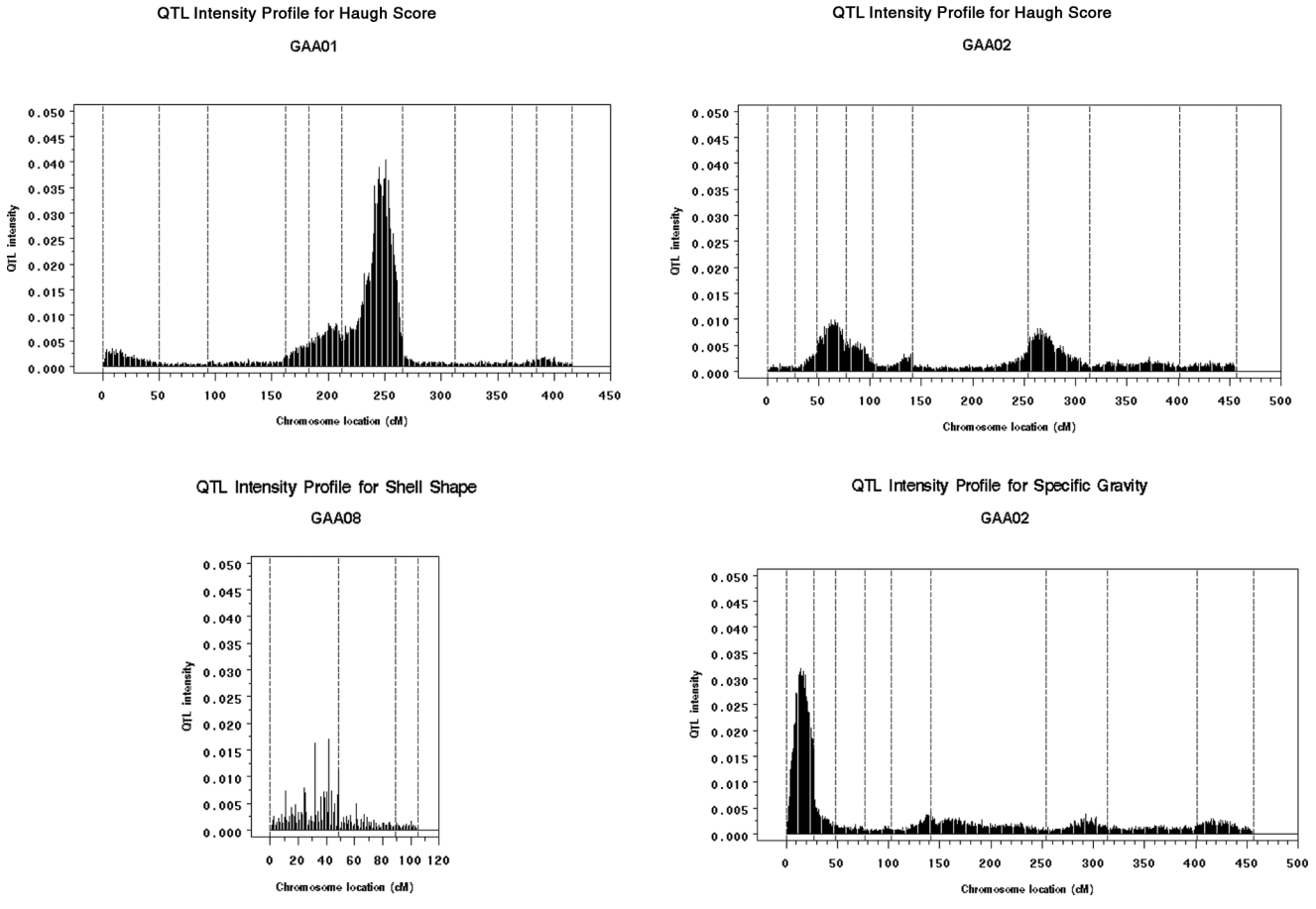

Figure 1 Chromosomal intensity profiles for QTL identified in a meat-type × layer-type cross.

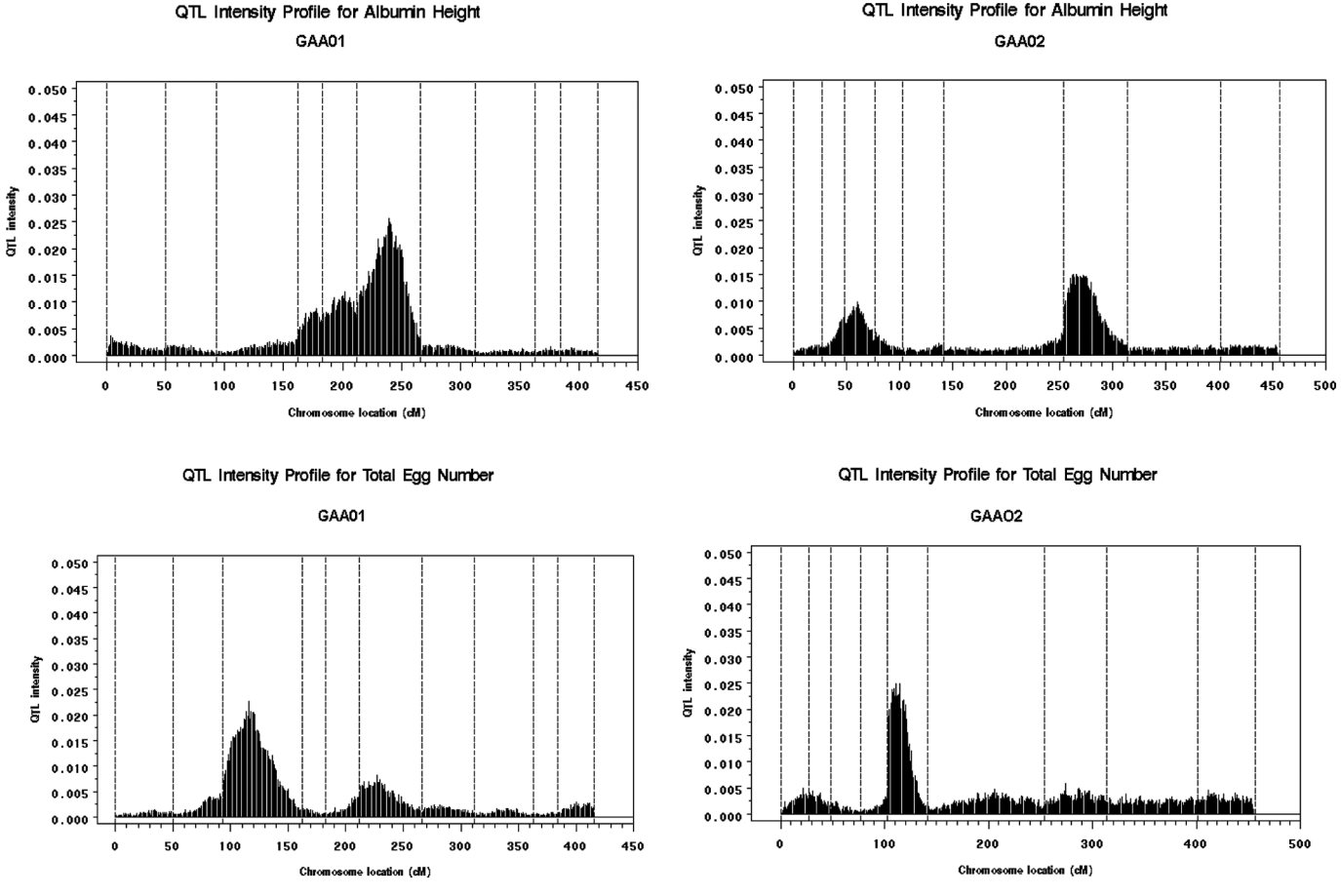

Figure 1 Continued.

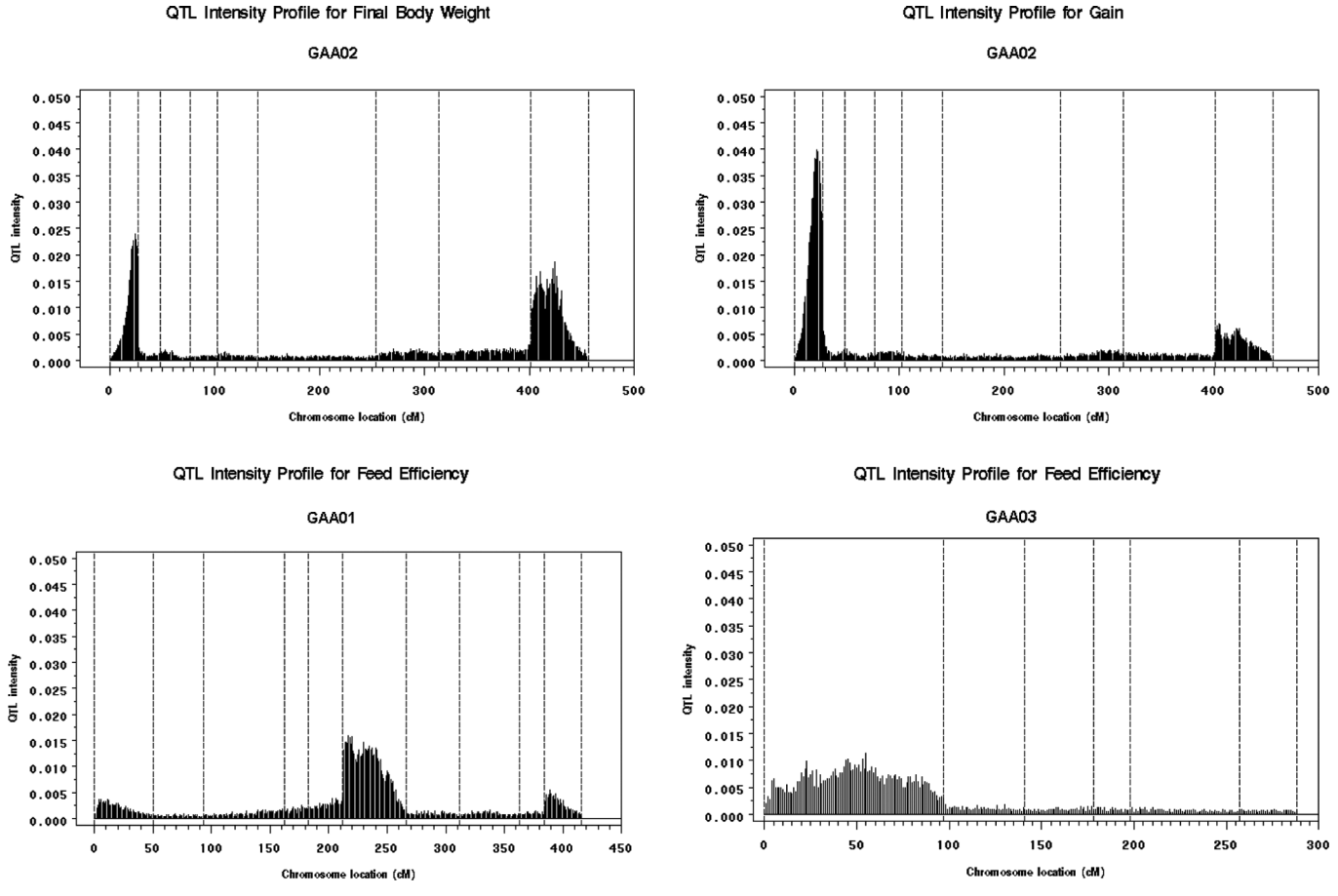

Figure 1 Continued.

The extent of the genome coverage in this study was limited for some linkage groups (Table 1), and as a result it was not possible to identify QTL regions on some of the smaller chromosomes and linkage groups. Therefore only the information for GGA01 to GGA08 was considered in this paper. It is important to note that we were dependent on mapped microsatellites available at the time the experiment was carried out and as such did our best to cover as much of the chicken genome as possible. Unfortunately, due to the lack of informative markers, gaps in coverage did occur, as is the case for most livestock QTL experiments.

In summary, the putative QTL that have been identified in this study afford us with some exciting opportunities. Not only will it be possible to fine-map these QTL by increasing the number of markers used for genotyping on the various chromosomes of interest, but their existence can also spur us to add more markers specifically to those areas where they are now lacking. This has been done in other species, but as yet not to any extent in chickens. It will also be of interest to examine whether these QTL can be shown to be segregating in a layer-type × layer-type or meat-type × meat-type cross.

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ABBREVIATIONS

ALB_HGT	albumin height measured in millimeters
cM	centiMorgans
EGGTOT	the sum of the eggs laid by a bird
EGG_WGT	egg weight recorded in grams
FEEDEFF	feed efficiency or gain/feed consumed
FINBWT	body weight in decagrams at the end of the test period (approx. 500 days of age)
HAUGH	Haugh score
INITBWT	body weight in decagrams at the beginning of the test period
QTL	quantitative trait loci
SGRAV	specific gravity recorded after subtracting from the actual specific gravity reading a 1.0 and multiplying the residual by 100
SHELSHAP	shell shape or the ratio of the width of the egg at its largest point to the egg's length at its longest point

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